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FORAGING PATTERNS OF FOREST BIRDS: MALE-FEMALE DIFFERENCES

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Abstract.—Foraging patterns of males and females of nine arboreal passerine bird species that occur syntopically in a northern hardwoods forest in New Hampshire were compared intra- and interspecifically. Males and females of each species were similar in morphology but often differed in foraging heights, use of foraging maneuvers and substrates, tree species in which foraging occurred, and in positions within trees where they attacked prey. Overall, intraspecific intersexual differences were less than interspecific ones. Two exceptions were the Scarlet Tanager (*Piranga olivacea*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), in which males of the two species were more similar to each other in methods of food exploitation than they were to conspecific females. This finding indicates the need to consider intraspecific (especially intersexual) variability, as well as interspecific differences, in studies of resource use and niche relations among forest birds.

Although differences between the sexes result in some resource partitioning within species, they are best explained by the hypothesis that birds forage locally near their centers of activity, which for passerine birds in the breeding season differ for males and females. Male foraging heights were positively correlated with song perch heights, as were female foraging heights with nest heights. Foraging heights of males, however, were not always higher than those of females, nor were mean song perch heights always higher than nest sites. Environmental factors such as local variations in the vertical distribution of plant species, vegetation structure, food availability, and predation are discussed as factors that affect the height at which these activities, and thus foraging, take place. *Received 24 Sept. 1985, accepted 22 Nov. 1985.*

Most attempts to characterize the foraging relations and associated niche characteristics of forest birds have not taken into account intraspecific variation in foraging, such as differences between the sexes (e.g., Rabenold 1978, Eckhardt 1979, Holmes et al. 1979, Landres and MacMahon 1983, Airola and Barrett 1985). This is due largely to the difficulties of clearly identifying in the field the sex of rapidly foraging individuals of the often monomorphic and monochromatic species occupying these habitats. Obtaining sufficient sample sizes for each sex can also be a problem.

Investigations of single species or small guilds, however, have shown that foraging patterns of males and females often differ, e.g., in species of woodpeckers (Kilham 1965, 1970; Selander 1966; Ligon 1968; Jackson 1970; Williams 1980), nuthatches (McEllin 1979, but see Grubb 1982), vireos (Williamson 1971), muscicapid flycatchers (Bell 1982), and several

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parulid warblers (Morse 1968, 1971, 1980; Busby and Sealy 1979; Morrison 1982; Franzreb 1983). The explanations most often given for such differences are that they represent either (1) the results of intraspecific resource partitioning (Rand 1952, Selander 1966, Robbins 1971) or (2) the operation of foraging constraints associated with reproductive or other sex-related activities, such as localized feeding of males near song perches and of females near nest sites (Morse 1968, 1980; Williamson 1971; Franzreb 1983).

The purposes of this paper are (1) to examine the foraging patterns and ecology of males and females of the nine most common species of arboreally foraging birds that occur syntopically during the breeding season in a northern hardwoods forest in central New Hampshire, and (2) to contrast intraspecific, intersexual patterns with those occurring between species. Specifically, do males and females of the same species exploit food resources in ways more similar to each other compared to those exhibited by other co-occurring species? If intraspecific differences exist, do they represent resource partitioning, the results of foraging constraints, or both?

STUDY AREA AND METHODS

The study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, on the 10-ha gridded census plot described by Holmes and Sturges (1975). The forest consists of second-growth northern hardwoods, with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) predominating. Occasional white ash (*Fraxinus americana*) and red spruce (*Picea rubens*) also occur. Canopy height averages about 25 m. The understory consists of saplings of the dominant tree species (except yellow birch), striped and mountain maples (*A. pensylvanicum* and *A. spicatum,* respectively), hobblebush (*Viburnum alnifolium*), a common fern (*Dryopteris spinulosa*), and various forbs.

Degrees of sexual dimorphism were assessed from measurements of weights, wing lengths, and culmen lengths of the males and females of each species. The first two of these measurements are often used as indicators of body size (Hamilton 1961), and the third is sometimes associated with differences in foraging between the sexes (Selander 1966). All weights were of live birds captured in mist nets on the study area during the breeding period and measured with Pesola scales (0.5-g accuracy). Weights of females caught prior to 16 June and of others known or suspected to be egg laying were excluded from the data set. Culmen and wing lengths of males and females of each species were measured with dial calipers (to 0.1 mm), either on live birds at Hubbard Brook or on specimens in the American Museum of Natural History that had been collected in summer in New England.

Foraging patterns of males and females were quantified between mid-June and mid-July in summers from 1974 to 1978. This coincided with the nestling and early fledging stage of the breeding cycle, which was the time when birds were foraging most actively and when food may have been scarcest (Holmes et al. 1979; R. T. Holmes, unpubl. data). The sex of each bird under observation was determined either by plumage (warblers, tanager, grosbeak) (see Table 1 for species considered in this study) or by the presence of unique individually coded color bands (all species, but especially the flycatcher and vireos). Color bands were

TABLE 1
MENSURAL CHARACTERISTICS OF MALE AND FEMALE PASSERINES AT HUBBARD BROOK

		Characteristic		
Bird species	Sex	Field weight (g)[a]	Culmen length (mm)	Wing length (mm)
Least Flycatcher (*Empidonax minimus*)	M	10.2 ± 0.7 (54)[b]	7.5 ± 0.2 (7)[a]	62.1 ± 0.5 (5)[a]
	F	9.9 ± 1.3 (95)[c]	7.3 ± 0.4 (14)[a]	60.0 ± 2.9 (13)[a,c]
Red-eyed Vireo (*Vireo olivaceus*)	M	17.2 ± 1.0 (112)	9.6 ± 0.3 (21)[a]	80.0 ± 2.2 (18)[a]
	F	17.2 ± 1.3 (111)	9.4 ± 0.5 (25)[a]	78.0 ± 1.8 (23)[a,d]
Philadelphia Vireo (*V. philadelphicus*)	M	11.4 ± 0.7 (13)	7.2 ± 0.2 (5)	66.2 ± 2.4 (5)
	F	12.0 ± 1.6 (13)	6.8 ± 0.2 (5)[d]	66.5 ± 1.2 (5)
Black-throated Blue Warbler (*Dendroica caerulescens*)	M	9.8 ± 0.5 (70)	7.3 ± 0.2 (11)[a]	63.8 ± 2.5 (9)[a]
	F	10.1 ± 0.9 (55)[c]	7.2 ± 0.3 (7)[a]	60.4 ± 0.5 (6)[a,d]
Black-throated Green Warbler (*D. virens*)	M	9.2 ± 0.5 (26)	7.3 ± 0.3 (6)	61.5 ± 0.9 (6)
	F	9.3 ± 0.6 (28)	7.1 ± 0.2 (5)	59.0 ± 1.5 (4)
Blackburnian Warbler (*D. fusca*)	M	9.8 ± 0.6 (15)	7.2 ± 0.2 (5)	67.9 ± 2.0 (5)
	F	10.4 ± 0.9 (12)	7.3 ± 0.3 (5)	64.6 ± 2.9 (5)
American Redstart (*Setophaga ruticilla*)	M	8.6 ± 0.5 (71)	6.9 ± 0.3 (13)[a]	63.2 ± 1.7 (10)[a]
	F	8.7 ± 0.6 (80)	6.9 ± 0.3 (12)[a]	59.5 ± 2.0 (9)[a,e]
Scarlet Tanager (*Piranga olivacea*)	M	28.7 ± 1.8 (22)	10.4 ± 0.6 (5)	94.5 ± 2.5 (5)
	F	29.6 ± 1.8 (30)	9.9 ± 0.5 (5)	91.3 ± 2.7 (5)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	M	43.6 ± 2.8 (18)	10.1 ± 0.9 (5)	104.5 ± 3.4 (5)
	F	45.5 ± 2.9 (21)	10.4 ± 0.5 (6)	99.1 ± 4.1 (6)[c]

[a] Measurements from live adult birds captured in mist nets at Hubbard Brook.

[b] $\bar{x}$ ± SD (N).

[c] Female differs from male (*t*-test, $P < 0.05$).

[d] Female differs from male (*t*-test, $P < 0.01$).

[e] Female differs from male (*t*-test, $P < 0.001$).

placed on birds caught in mist nets that were operated weekly each season as part of censusing procedures (see Holmes and Sturges 1975). By the end of each nesting season, more than 80% of the adult birds on the study area were individually marked. Mist-netted birds were sexed by the presence of a cloacal protuberance (male) or brood patch (female), following the procedures of Wood (1969) and the U.S. Fish and Wildlife Service Banding Manual (1977).

Methods used to quantify bird foraging behavior have been described by Holmes et al. (1979). Briefly, individual birds were followed for as long as they could be kept in sight (usually <2 min), and all attempts to capture prey were recorded. For each prey-attack, we noted the maneuver used (glean, hover, hawk; see below), the substrate to which it was directed (bark, leaf, ground, air), the plant species when appropriate, the height above ground, and, if in a tree, whether it was proximal to the main axis (trunk) or distal (along the outer halves of branches). At least six to eight individuals of each sex per species, and often more for the more common species, were observed each season.

Data on nest heights were collected in the summers of 1969 through 1979 in the study area. Heights of song perches used by males were estimated in June 1983 and 1984. For these, the height of a singing male was recorded once per encounter, except for the less-common species, for which up to five records were taken per individual at intervals of not less than 5 min.

Two statistical tests were used to compare males and females within species. Differences between means (weights, morphological measurements, foraging heights) were analyzed with Student's *t*-tests. Differences between frequency distributions (foraging maneuvers, tree species use, foraging height distributions, foraging locations within trees) were compared with *G*-tests (Sokal and Rohlf 1981). The level of significance was 0.05 (see Discussion). Overlap values of foraging height distributions were calculated using the method of Holmes and Pitelka (1968).

To compare foraging among sexes and species simultaneously, multivariate techniques were used on a matrix of 18 "species" (rows) by 22 "characters" (columns), following the procedures of Holmes et al. (1979). In this case, the "species" represent males and females of nine passerine bird species. The characters are similar to the categories used in the earlier analysis (Holmes et al. 1979), except that maneuvers directed towards the ground, tree trunks, and other actions infrequently used by these foliage-foragers were omitted. In the present analysis, the 22 characters included nine maneuver-substrate categories, proportional use of eight plant species, two foraging location categories (proximal vs distal), mean foraging height, standard deviation of foraging height, and mean body weight. The justifications for selecting these characters are given in Holmes et al. (1979). The first 19 characters represent use frequencies of foraging categories and were log-transformed to reduce skewness. All 22 columns were standardized to bring means to 0 and variances to 1.0 (see Holmes et al. 1979), the effect of which is to weight all categories equally. The 22 × 18 "species" matrix (Q-technique of Sneath and Sokal 1973) was used to calculate the Euclidean distances between all combinations of the 18 "species" in the multidimensional space defined by the 22 characters. This distance matrix was then subjected to hierarchical cluster analysis (maximum method, Johnson 1967) to illustrate graphically the similarities and differences in foraging among the sexes and species of these forest birds.

RESULTS

The Species and Their Intersexual Morphological Differences

The nine species of passerine birds at Hubbard Brook considered in this paper consisted of a tyrannid flycatcher, two vireos, four parulid warblers, a tanager, and a grosbeak (Table 1). All take more than 50% of their prey from tree foliage and comprise the major component of the foliage-gleaning-hovering guild in this forest (Holmes et al. 1979). Three species (Least Flycatcher, Red-eyed Vireo, Philadelphia Vireo) are sexually monochromatic, and the other six are sexually dichromatic, with males having brighter coloration than females. All have basically monogamous breeding systems (Ford 1983).

Measurements of body weights, culmen lengths, and wing lengths of the males and females of these nine species were examined for evidence of sexual dimorphism (Table 1). Only the Least Flycatcher and Black-throated Blue Warbler exhibited statistically significant differences in weight between the sexes (Table 1), with the male being heavier in the flycatcher, and the female heavier in the warbler. In both cases, these differences amounted to <3%. Intersexual differences in wing lengths were more frequent, with the males of six species having significantly longer wings than their respective females. Differences, however, were small (6% or less), relative to those occurring among "strongly dimorphic" species such as raptors or some icterids (Selander 1966). The only species to show a significant sex-related difference in culmen length was the Philadelphia Vireo. In that species, males had a slightly longer bill (Table 1).

Thus, for these species overall, only minor sexual dimorphism is evident, and the differences that exist do not seem to be sufficient to have major effects on food capturing abilities or other aspects of food resource exploitation.

Use of Vertical Strata

Foraging heights.—Mean foraging heights of males and females of all but one species ranged between 10 and 15 m (Table 2). The large standard deviations of foraging heights (Table 1) and broad foraging-height profiles (Fig. 1) of each sex of these eight species indicate that they foraged over practically the entire vertical profile of this forest. The single species with a relatively narrow foraging height range was the Black-throated Blue Warbler. It foraged primarily in the shrub and sapling layers; males at an average height of 6 m and females at 3 m (Table 2) (Fig. 1).

For three species (Least Flycatcher, American Redstart, Blackburnian Warbler), mean foraging heights of males and females were statistically similar, while in six, significant intersexual differences were found (Table 2). In four of these (Red-eyed Vireo, Black-throated Green Warbler, Scarlet Tanager, Rose-breasted Grosbeak), females foraged higher than males, and in two (Philadelphia Vireo and especially the Black-throated Blue Warbler), males foraged higher than females (Table 2).

Because the vertical foraging distributions of these birds often were not distributed normally (Fig. 1), comparisons of means are not always valid. Therefore, I compared the intersexual distributions of foraging heights (see Fig. 1) using *G*-tests (Sokal and Rohlf 1981). The results showed significant differences ($P < 0.01$) in the use of strata for foraging by males and females of all species except the grosbeak (Table 2). Three species showed significant differences in foraging height distributions but had statistically similar mean foraging heights. In the redstart and especially

TABLE 2

VERTICAL DISTRIBUTION (M) OF FORAGING, SINGING, AND NESTING BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

Bird Species	Sex	Foraging heights	% Overlap[a]	Song perch heights	Nest heights
Least Flycatcher	M	10.5 ± 4.2 (287)[b]	79.2[f]	7.5 ± 2.3 (20)	11.8 ± 4.8 (85)
	F	10.4 ± 4.8 (324)			
Red-eyed Vireo	M	11.8 ± 4.5 (739)	87.9[f]	14.5 ± 4.6 (57)	10.7 ± 5.8 (31)
	F	12.5 ± 4.3 (424)[d]			
Philadelphia Vireo	M	14.6 ± 6.2 (388)	78.9[f]	15.9 ± 4.9 (45)	24.0 ± 4.6 (14)
	F	13.5 ± 7.3 (195)[c]			
Black-throated Blue Warbler	M	5.9 ± 3.8 (884)	62.7[f]	8.1 ± 3.8 (47)	0.5 ± 0.2 (17)
	F	3.3 ± 3.0 (470)[e]			
Black-throated Green Warbler	M	13.1 ± 5.2 (442)	78.7[f]	15.1 ± 2.6 (36)	11.3 ± 4.0 (9)
	F	15.2 ± 4.0 (270)[e]			
Blackburnian Warbler	M	15.1 ± 3.5 (324)	72.8[f]	13.4 ± 4.1 (23)	7.3 ± 3.2 (3)
	F	14.4 ± 4.8 (320)			
American Redstart	M	10.9 ± 4.8 (1111)	88.6[f]	11.1 ± 2.9 (33)	7.4 ± 4.4 (70)
	F	11.3 ± 4.6 (510)			
Scarlet Tanager	M	11.7 ± 4.8 (303)	59.8[f]	15.5 ± 4.9 (33)	12.8 ± 3.2 (8)
	F	14.8 ± 4.5 (137)[e]			
Rose-breasted Grosbeak	M	10.8 ± 5.3 (189)	81.4	12.0 ± 4.8 (26)	14.5 ± 8.8 (12)
	F	12.9 ± 5.4 (99)[d]			

[a] Overlap between male and female foraging distributions (see Fig. 1), calculated by 2-m intervals using the method of Holmes and Pitelka (1968).

[b] $\bar{x}$ ± SD (N).

[c] Female differs from male (*t*-test, $P < 0.05$).

[d] Female differs from male (*t*-test, $P < 0.01$).

[e] Female differs from male (*t*-test, $P < 0.001$).

[f] Female differs from male (*G*-test, $P < 0.01$).

the Blackburnian Warbler, females used a higher stratum proportionately more often than did males (Fig. 1), resulting in significantly different profiles, even though mean heights were not statistically different (Table 2). The opposite pattern was found for the Least Flycatcher: females used a lower stratum more frequently than males (Fig. 1). In every case, however, the overlap in vertical foraging distribution between males and females of each species was extensive (Fig. 1), ranging from 62% in the Black-throated Blue Warbler to 89% in the American Redstart (Table 2).

Song perch and nest heights.—Heights at which males sang ranged from an average of 8.1 m for the Black-throated Blue Warbler to 15.9 m for the Philadelphia Vireo (Table 2). Mean heights of song perches correlated significantly with the mean foraging heights of males ($r = 0.74$, $P < 0.05$).

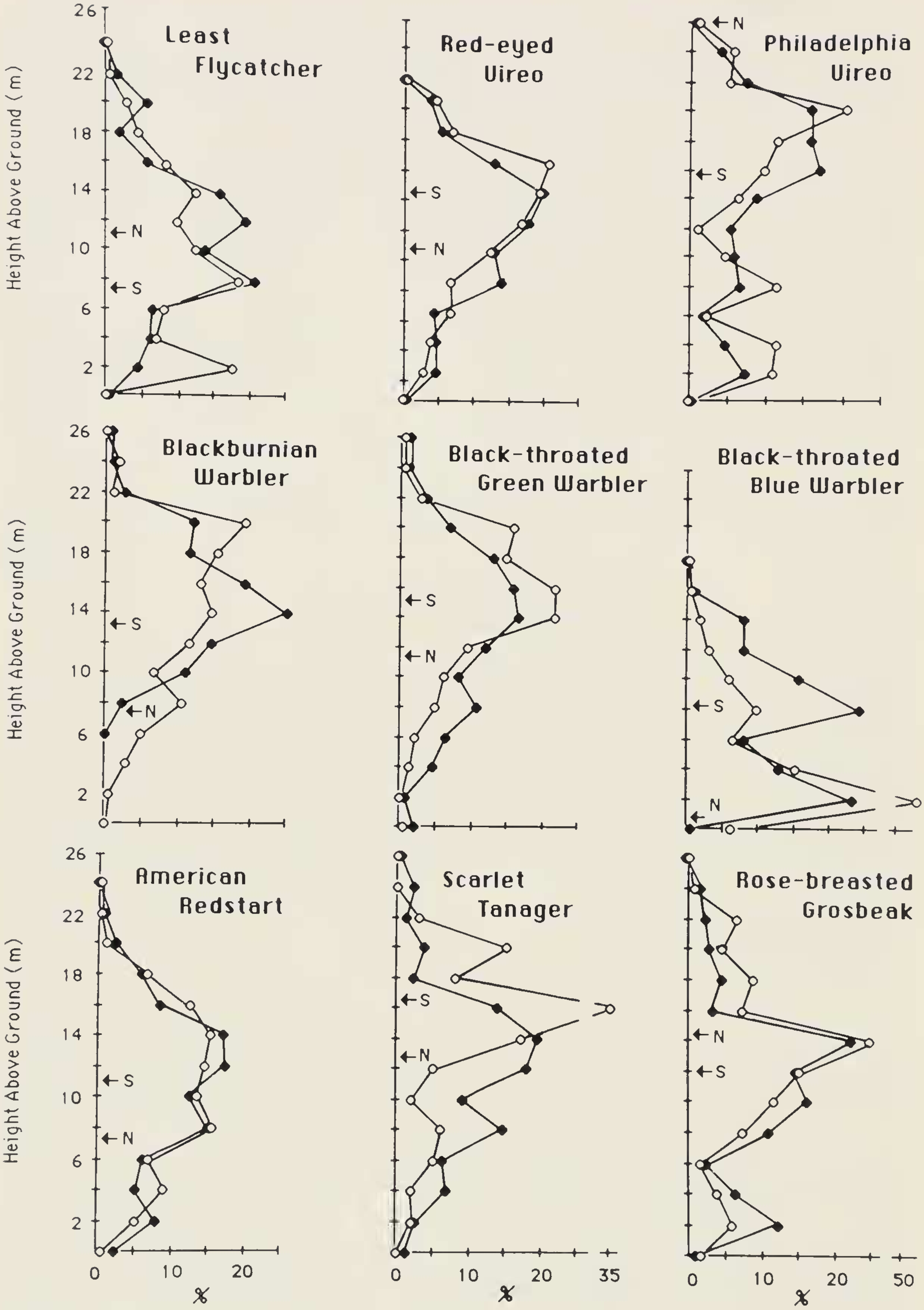

FIG. 1. Foraging height distributions by 2-m intervals for males (solid symbols) and females (open symbols) of nine passerines breeding in the Hubbard Brook forest. Sample sizes are given in Table 2. N = mean nest height and S = mean singing height of males (see Table 2).

They were slightly more correlated with the mean foraging heights of conspecific females ($r = 0.79$, $P < 0.05$).

Nesting heights varied from an average of 0.5 m for the Black-throated Blue Warbler to 24 m for the Philadelphia Vireo (Table 2). There was a positive but nonsignificant correlation between nest heights and foraging heights of females ($r = 0.62$, $P > 0.08$) and of males ($r = 0.62$, $P > 0.08$).

Use of Foraging Substrates and Maneuvers

The foraging behavior of males and females of each species, as indicated by their prey-attack behavior and the substrates to which they were directed, was broadly similar (Table 3). Thus, both sexes of the two vireos, the flycatcher, redstart, Black-throated Blue Warbler, and tanager were primarily leaf hoverers, while male and female Black-throated Green Warblers, Blackburnian Warblers, and Rose-breasted Grosbeaks were mainly leaf gleaners. The second most common maneuver-substrate combination used was the same for both sexes in each species, except for the tanager, in which males gleaned and females hawked flying insects (Table 3). The second most common foraging action within each species was usually another leaf-directed attack (e.g., leaf gleaners hovered secondarily at leaves and vice versa), but for the flycatcher, redstart, and female tanager, it was hawking of flying insects. Despite overall similarities within species, there were significant intersexual differences in seven of the species in their use of maneuver-substrate categories. Only males and females of the Least Flycatcher and of the Philadelphia Vireo were statistically indistinguishable (Table 3).

Foraging on Plant Species and Locations within Trees

Holmes and Robinson (1981) showed that many of the bird species at Hubbard Brook forage selectively among the different tree species in the forest, and similar observations have been reported for other forest birds (e.g., Franzreb 1983, Airola and Barrett 1985). When the foraging attack frequencies of males and females of Hubbard Brook birds are analyzed by major tree species to which they were directed (using only plant-directed prey-attacks), significant intersexual differences were found in all species except the Least Flycatcher and Scarlet Tanager (Table 4). Although the proportion of foraging maneuvers occurring in different tree species was basically consistent between males and females of each bird species, some differences occurred. Male Black-throated Green Warblers foraged on sugar maple and yellow birch about equally, while females used yellow birch more often than sugar maple (Table 4). Male grosbeaks foraged with about equal frequency on beech, sugar maple, and yellow birch, but females foraged more often on yellow birch, and seemed to

TABLE 3

USE OF FORAGING SUBSTRATES AND MANEUVERS BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

			% Frequency									
			Leaf		Twig		Branch		Trunk		Air	Ground
Bird species	Sex	N	Hover	Glean	Hover	Glean	Hover	Glean	Hover	Glean	Hawk	All[a]
Least Flycatcher	M	262	72.5	1.9	0	0.4	0.4	0.4	0.4	0.4	23.2	0
	F	287	81.6	2.4	0	0.3	1.4	0	0	0	14.3	0
Red-eyed Vireo	M	664	50.2	33.4	2.4	1.8	1.1	2.9	2.0	0.9	5.3	0
	F[b]	397	44.8	42.5	0.5	0.5	1.3	1.3	0.5	0.3	8.3	0
Philadelphia Vireo	M	334	58.4	27.6	0	2.0	1.5	2.3	1.5	0.9	5.2	0.6
	F	169	55.0	30.2	0	1.2	1.8	4.1	0	0	7.7	0
Black-throated Blue Warbler	M	888	50.3	21.0	1.4	4.4	1.4	5.4	4.3	4.3	7.4	0.1
	F[b]	471	55.5	24.0	0.2	1.9	0.4	1.9	3.4	4.8	6.8	1.1
Black-throated Green Warbler	M	384	33.8	43.0	1.0	2.6	0.5	0.8	2.1	3.9	10.7	1.6
	F[b]	233	21.0	52.5	2.6	6.4	1.3	2.1	2.1	1.3	10.7	0
Blackburnian Warbler	M	283	18.8	56.5	0.4	3.5	0.4	3.1	1.4	7.8	8.1	0
	F[c]	254	27.0	49.1	0	8.8	0.4	1.3	1.8	1.3	10.3	0
American Redstart	M	911	47.4	16.1	0.1	0.2	0.2	3.3	0.7	0.9	30.7	0.4
	F[b]	432	60.4	15.0	0.2	0.5	0.5	0.5	0.2	0.2	22.5	0
Scarlet Tanager	M	166	34.9	28.9	0	1.2	3.1	8.4	6.0	2.4	14.5	0.6
	F[c]	81	34.6	28.4	0	0	0	4.9	1.2	0	30.9	0
Rose-breasted Grosbeak	M	280	26.4	47.5	0.4	2.1	1.1	3.2	6.4	6.4	6.1	0.4
	F[c]	128	34.2	51.6	0	1.6	0	1.6	1.6	1.6	6.3	2.3

[a] Includes all ground-directed maneuvers, such as gleans, hovers, probes, etc. Data in this column were not included in the multivariate analyses.

[b] Female differs from male (*G*-test, $P < 0.001$).

[c] Female differs from male (*G*-test, $P < 0.01$).

TABLE 4

FREQUENCY (%) OF FORAGING MANEUVERS DIRECTED TOWARDS PREY ON DIFFERENT PLANT SPECIES BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

Bird species	Sex	N	Plant species							
			Beech	Sugar maple	Yellow birch	White ash	Conifer	Other maple[a]	Viburnum	Herb-fern
Least Flycatcher	M	235	23.1	35.7	35.7	0.4	0.9	3.8	0	0.4
	F	286	22.7	41.6	30.5	0.4	0.7	3.1	0	1.0
Red-eyed Vireo	M	697	29.4	44.9	20.9	2.0	1.3	1.5	0	0
	F[b]	390	29.5	35.6	26.9	5.4	0.5	2.1	0	0
Philadelphia Vireo	M	358	10.1	33.0	40.8	12.0	1.1	2.0	0	1.1
	F[b]	186	9.1	23.7	40.9	20.4	0.5	4.3	1.1	0
Black-throated Blue Warbler	M	873	33.0	32.4	10.3	0	2.5	12.9	8.7	0.2
	F[b]	470	30.2	25.4	9.4	0.4	2.3	10.2	18.7	3.4
Black-throated Green Warbler	M	389	10.0	38.6	39.8	0.8	9.3	1.5	0	0
	F[c]	242	4.5	12.4	74.4	0.4	5.0	2.9	0.4	0
Blackburnian Warbler	M	300	14.0	7.3	65.4	2.0	10.0	1.3	0	0
	F[c]	294	8.5	5.8	52.4	3.7	29.6	0	0	0
American Redstart	M	865	20.9	36.0	33.0	0.7	0.7	5.8	0.1	2.5
	F[c]	450	25.1	44.0	26.2	0.2	0.7	3.1	0	0.7
Scarlet Tanager	M	159	30.8	18.9	47.8	0.6	0	1.9	0	0
	F	73	28.8	12.3	45.2	2.8	8.2	2.7	0	0
Rose-breasted Grosbeak	M	282	31.6	29.1	31.0	0.7	0	5.3	1.4	0
	F[c]	125	8.0	29.6	47.2	12.0	1.6	1.6	0	0

[a] *Acer spicatum* and *A. pensylvanicum* (see Study Area and Methods).
[b] Female differs from male (*G*-test, $P < 0.01$).
[c] Female differs from male (*G*-test, $P < 0.001$).

TABLE 5
FREQUENCY OF PREY-ATTACKS BY MALE AND FEMALE PASSERINES[a] DIRECTED TOWARDS SUBSTRATES ALONG THE DISTAL HALVES OF BRANCHES OF CANOPY TREES

Bird species	% Distal	
	Males	Females
Least Flycatcher	78.9 (147)[b]	79.9 (199)
Red-eyed Vireo	58.5 (388)	61.3 (253)
Philadelphia Vireo	61.8 (152)	70.3 (74)
Black-throated Green Warbler	61.1 (167)	74.2 (177)[c]
Blackburnian Warbler	77.3 (185)	80.0 (170)
American Redstart	68.7 (419)	64.7 (249)
Scarlet Tanager	29.3 (99)	64.6 (48)[c]
Rose-breasted Grosbeak	51.0 (143)	52.5 (61)

[a] The Black-throated Blue Warbler is not included because it forages primarily among shrubs and saplings in the understory where the distinction between proximal and distal is not easily made.

[b] % (N).

[c] Females differ from males (*G*-test, $P < 0.01$).

avoid beech (Table 4). Female Black-throated Blue Warblers foraged more frequently than males on hobblebush, herbs, and ferns (Table 4). Finally, although male and female Blackburnian Warblers attacked prey predominately on yellow birch foliage, females attacked prey in conifers nearly a third of the time, considerably more than did males (Table 4). The latter is an example of high selectivity, because conifers in this forest are relatively rare (relative importance value = 1%, Holmes and Robinson 1981).

Males and females of each species foraged with equal frequency in the proximal and distal portions of canopy trees, except for the Black-throated Green Warbler and Scarlet Tanager (Table 5). (Black-throated Blue Warblers were not considered in this analysis; see footnote in Table 5.) In these two species, females foraged more often in the distal, and males more often in the proximal, parts of trees. This was especially pronounced in the tanager, in which males foraged 70% of the time in the inner portions of the trees (Table 5) and took insects relatively more often from bark than did females (Table 3). Female tanagers and all other species foraged most often in the distal portions of trees where most foliage (and thus foliage-dwelling insects) occurred.

Inter- and Intra-specific Comparisons

The clustering of the males and females in multivariate space, based on 22 foraging-related characteristics (see Methods section), illustrates their similarities and differences in foraging both between sexes within species and between species within sex (Fig. 2). Despite many statistically

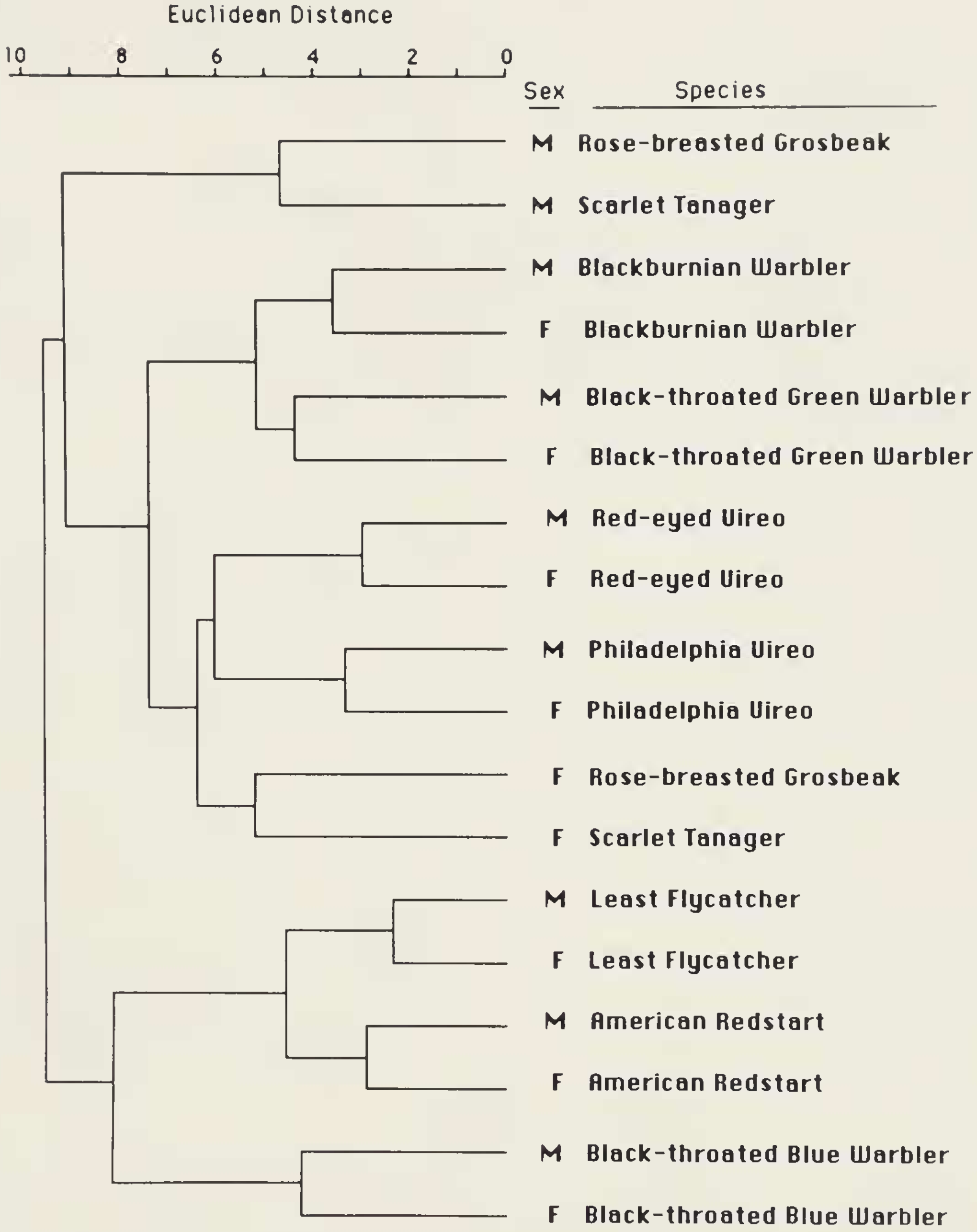

FIG. 2. Cluster dendrogram showing intersexual and interspecific relationships of nine passerine birds at Hubbard Brook, based on multivariate analyses of their foraging behavior.

significant intersexual differences in individual characteristics within species, conspecific males and females were generally more similar to each other than they were to other species. The two exceptions were the Scarlet Tanager and Rose-breasted Grosbeak, in which males were more similar to each other than to their respective females. The females of these two species were more closely aligned with the vireos than they were with the males of their own species (Fig. 2). These associations are due to the females of both species foraging, on average, higher in the canopy (Table

2) and more frequently in white ash (Table 4) than did males, while males of the two species attacked prey on trunks and branches more often than did females (Table 3).

DISCUSSION

The results of this study indicate that considerable intersexual variation in resource exploitation exists within insectivorous bird species at Hubbard Brook, and that it occurs in the absence of any major morphological differences between the sexes. Before discussing the implications of these findings, two caveats concerning the statistical procedures and results need to be mentioned.

First, because many single statistical tests were performed, some may show significance simply by chance (i.e., a Type I error, Sokal and Rohlf 1981). However, even if a more stringent significance level were to be accepted (e.g., $P < 0.01$), most of the conclusions would hold (see Results). Secondly, and potentially more important, is the problem of "sacrificial pseudoreplication" that is coupled with the use of Chi-square (or *G*) tests (see Hurlbert 1984). When data are pooled prior to statistical analysis, as they were for the foraging parameters in this study, no measure of variance is possible and statistical results may be spurious. In the present study, the data came from a variety of individuals of both sexes observed during a three to four week period in each of several seasons. These features, along with the relatively large sample sizes, should swamp out the above sampling effects. Nevertheless, the statistical results for some of the differences between the sexes should be viewed with caution, and future studies should be designed to include proper replication and measures of variability. As far as I am aware, no published studies of bird foraging behavior have been so designed.

Two major hypotheses have been proposed to account for the existence of differences in foraging between male and female forest passerines. The first is that they have evolved as a result of, or to alleviate, intraspecific competition (Rand 1952, Selander 1966). Although the causal factors implicit in this hypothesis can not be tested adequately with available data (see above), the males and females of these species do often forage in different places or different ways, i.e., partition resources. Only the Least Flycatcher showed few intersexual differences (Tables 2–5). Sexes of other species differed in the use of at least two or more foraging categories, e.g., in foraging maneuvers, the heights at which they foraged, the plant species they searched for insects, and their positions of foraging within trees. Moreover, for species in which males and females foraged at the same heights (e.g., American Redstart), there were often differences in maneuver-substrate and tree species use, while among species in which sexes foraged at different heights (e.g., Philadelphia Vireo), there were no differences in maneuver-substrate use.

Even though males and females often differed in patterns of food exploitation, they were generally more similar in their foraging behavior to each other than to other species. Similar findings were reported by Morse (1971) for *Dendroica* warblers in Maine. However, at Hubbard Brook, there were two exceptions to these patterns: male Scarlet Tanagers and Rose-breasted Grosbeaks were more similar to each other in how they foraged than they were to their conspecific females. Thus, studies of foraging behavior and niche relations should consider differences between the sexes in order to document accurately the ecological similarities and differences within forest bird guilds. This holds even if only a few species show such marked differences.

The second hypothesis for the existence of intersexual differences is that birds forage near their centers of activity, which for passerine birds in the breeding season differ between the sexes. The most frequent intersexual foraging difference reported in previous studies has been that males typically foraged higher than females (Morse 1968, Williamson 1971, Busby and Sealy 1979, McEllin 1979, Morrison 1982, Franzreb 1983, but see Grubb 1982 and Bell 1982). Some researchers have suggested that this is because males are more conspicuous and effective in long distance communication when they are at greater heights and that they feed near their song perches; likewise, females forage in lower strata near their nest sites (Morse 1968, 1980; Franzreb 1983; and others). The results from Hubbard Brook appear at first to contradict this hypothesis. Males of only two species foraged significantly higher than females, there were no significant differences in mean foraging heights between sexes in three species, and females foraged significantly higher than males in four species. The pattern was variable even for the *Dendroica* warblers, for which previous studies had indicated that males always foraged higher than females (Morse 1968, Busby and Sealy 1979, Morrison 1982, Franzreb 1983): at Hubbard Brook, males foraged significantly higher than females in only one species (Black-throated Blue); the pattern was reversed in another (Black-throated Green); and there was no significant difference in male-female foraging heights in the third (Blackburnian) (Table 2).

Nonetheless, male foraging heights for all nine species at Hubbard Brook were positively correlated with male song perch heights, and those of females with nest heights. Although nest height in six species averaged lower than the male's singing height, the differences were large only for the Black-throated Blue and Blackburnian warblers (Table 2). For the remaining three species and particularly the Philadelphia Vireo, nests were placed, on average, higher than male song heights (Table 2) (Fig. 1).

Most previous studies showing that males foraged higher than females (e.g., Morse 1968, McEllin 1979, Morrison 1982, Franzreb 1983, but not Williamson 1971) were conducted in coniferous or mixed deciduous-coniferous habitats. Males in these studies often sang from near the tops of conically-shaped, densely foliated conifers, and females nested lower in the thicker foliage (Morse 1980). In broad-leaved forests, such as those at Hubbard Brook, there is typically a dense, closed canopy, a relatively open subcanopy, an an understory that may vary in foliage density (see foliage density profile for the Hubbard Brook forest in Sherry 1979). In such habitats, as evidenced by the present study, birds often nest in dense foliage on or near the ground or in the canopy (Table 2), and males of many species forage and sing in the lower portions of the canopy and in the subcanopy (e.g., Least Flycatchers, American Redstarts, Black-throated Blue Warblers at Hubbard Brook, in particular) (Table 2). Thus, the principle that males forage in strata where they are relatively conspicuous and females forage near their nests applies to Hubbard Brook, but the particular structure of the forest influences the heights at which these events take place.

The fact that male and female passerines often forage at different heights (males higher than females or vice versa) means that each may encounter different foraging opportunities, which, in turn, may affect their foraging patterns (Robinson and Holmes 1982, 1984). Variability in foraging behavior among individual male and female American Redstarts has been attributed to local differences in vegetation structure and food availability on different territories (Holmes et al. 1978). Similar differences may occur within territories in areas frequented by males and females. One factor that may be important in this regard is the tree species present in the strata in which each sex does most of its foraging. Holmes and Robinson (1981) showed that birds at Hubbard Brook preferentially seek prey among the foliage of particular plant species. As some of these plant species are confined to or more abundant in particular strata, this may lead to differential foraging by height-separated male and female passerines. Examples at Hubbard Brook are the use of shrub-layer plant species, such as hobblebush and ferns, as foraging substrates by low-foraging female Black-throated Blue Warblers (Table 4) and the greater use of ash and yellow birch foliage, which occurs most abundantly in the upper canopy, by high-foraging female Philadelphia Vireos (Tables 2–4). Similar height-related differences in plant species use were noted by Franzreb (1983) for foraging male and female Yellow-rumped Warblers (*D. coronata*).

Another factor that might influence the foraging heights of male and female passerines is the presence and activity of predators. In some years at Hubbard Brook, chipmunks (*Tamias striatus*), Blue Jays (*Cyanocitta* *cristata*), and Sharp-shinned Hawks (*Accipiter striatus*) have been more abundant, and have significantly influenced the nesting success of birds (R. T. Holmes and T. W. Sherry, unpubl. data). In years when predators are abundant, their activity may influence the heights and locations of nests, which could, in turn, affect where birds forage.

Differences in the ways these male and female passerine birds exploit their food resources can therefore best be explained by height-related breeding activities. The extent to which these differences are genetically determined or learned is not known. A recent manipulative study by Peters and Grubb (1983), however, demonstrated experimentally that differences in foraging between male and female Downy Woodpeckers (*Picoides pubescens*) in winter were due to females actively avoiding the foraging microhabitats used by dominant males. Similar experimental and field studies would help clarify how labile or fixed these sexual differences in foraging are among forest passerines.

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